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# Mortality estimates from size distributions: A critique of Smith's model[1]

Smith (1972) described a method of computing mortality rates from growth and size-frequency data for a population which meets the following assumptions—

1. Instantaneous mortality rate, $m$, is constant.

2. Growth of individuals follows the Brody-Bertalanffy growth curve (Ricker 1975).

3. The population is stationary: recruitment is constant and occurs at size and age 0.

Smith defined $N(a)$ and $s(a)$ as the number and body length respectively, of organisms aged $a$, and he assumed $N(0) = 1$.

He then stated that assumptions 1–3 lead to the following equations—

$$N(a) = e^{-ma}; \tag{1}$$

$$s(a) = s_\infty(1 - e^{-ka}). \tag{2}$$

In Eq. 2, $s_\infty$ and $k$ are the asymptotic size and rate parameters, respectively, of the Brody-Bertalanffy growth function.

The two equations are combined by eliminating $a$ from both, resulting in the expression

$$\log_e N(a) = \frac{m}{k} \log_e \left[\frac{s_\infty - s(a)}{s_\infty}\right]. \tag{3}$$

According to Smith, Eq. 3 describes a population size distribution if assumptions 1–3 are met. For a specific population, he would first obtain estimates of $k$ and $s_\infty$ from growth data. Then pairs of observations $[s(a), N(a)]$ are taken from the size distribution to provide a regression estimate for $m/k$ via Eq. 3, from which $m$ can be computed.

The problem in using Eq. 3 is that its derivation requires the values $N(a)$ to be the relative frequencies of organisms in equal *age* intervals, but size-frequency data are usually based on equal *size* intervals. Because individual growth rates change with size and age, equal intervals along an age gradient translate into unequal size intervals.

In Eq. 1, $N(a)$ should be interpreted as the number *density*, rather than total numbers, of individuals aged $a$. The concept of number density, analogous to that of probability density, implies that $N(a)\Delta a$ is the total number of individuals in the thin age interval $(a,\ a + \Delta a)$ (Keyfitz 1968).

Thus, the number of individuals in an interval $(a,\ a + \Delta a)$ can be represented by the number density, $N(a)$, only if $\Delta a$ is the same for each interval. Likewise, the relative numbers in a size interval $(s,\ s + \Delta s)$ can be represented by the number density $N^*(s)$ from the continuous size distribution only if each size interval has an equal width, $\Delta s$.

By using a population model that deals directly with the number density, $N^*(s)$, I have shown (Van Sickle 1977) that the slope of the size distribution of any stationary population is described by

$$\frac{dN^*(s)}{ds} = -\left[\frac{g'(s) + m(s)}{g(s)}\right] N^*(s), \tag{4}$$

where $g(s) = ds/da$ = size-specific growth rate; $g'(s) = d[g(s)]/ds$; and $m(s)$ = size-specific instantaneous mortality rate.

Under Smith's assumption 1, $m(s) = m$, a constant. From assumption 2, the growth rate is obtained by differentiating Eq. 2 and eliminating the variable $a$.

This gives $g(s) = k(s_\infty - s)$ and $g'(s) = -k$.

Substitution into Eq. 4 results in

$$\frac{dN^*(s)}{ds} = \left[\frac{k - m}{k(s_\infty - s)}\right] N^*(s). \tag{5}$$

For comparison with Smith's estimation formula, Eq. 5 can be rewritten as

$$\frac{d[\log_e N^*(s)]}{d\left[\log_e\left(\frac{s_\infty - s}{s_\infty}\right)\right]} = \frac{m}{k} - 1. \tag{6}$$

[1] This study was supported by a National Research Council Research Associateship.

The equivalent form of Eq. 3 is

$$\frac{\mathrm{d}[\log_e N(a)]}{\mathrm{d}\left\{\log_e\left[\frac{s_\infty - s(a)}{s_\infty}\right]\right\}} = \frac{m}{k}. \quad (7)$$

Equation 6 gives the correct expression for $m/k$ when $N^*(s)$ represents relative numbers in equal length intervals, while Eq. 7 or 3 could be used if the frequency distribution were based on equal age classes. Of course, if a distribution with equal age classes is available, then Eq. 1 can be used to compute $m$, and growth information is unnecessary.

Allen (1967) has also distinguished between samples from size distributions and those from age distributions, and he derived expressions equivalent to Eq. 6 and 7. In addition, Allen presented estimation formulae for $m$ when growth in length or weight is exponential. Equation 4 can be used to obtain estimates for $m$ with any size measure, $s$, and growth curve, $g(s)$, and the assumption of stationarity.

The magnitude of the estimation error for $m$ due to the use of Eq. 3 or 7 rather than 6 depends on the corresponding estimate for $k$. Smith used an altered form of Eq. 3 to compute $m$ for 15 populations of calcareous marine organisms. Of these estimates, eight are too low by a factor of at least two when compared with values obtained from Eq. 6.

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